

Amphibian assemblages in zero-order basins in the Oregon Coast Range¹

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Abstract: Zero-order basins, extending from ridgelines to the initiation of first-order streams, were sampled in the Coast Range of Oregon to (i) characterize spatial distribution patterns of amphibian species and assemblages along longitudinal and lateral gradients, and relative to three geomorphic surfaces (valleys, headmost areas, and slopes); and (ii) develop empirical species–habitat models. Unmanaged zero-order basins were hotspots for amphibian diversity, with significant differences across geomorphic gradients. Captures of riparian-associated amphibians were higher in valley areas, usually within 2 m of basin center. Upland-associated amphibians were captured two times farther from basin centers than riparian-associated species, but highest densities occurred only 2–5 m from basin center. The most useful empirical models related captures of individual amphibian species to geomorphic, disturbance, moisture, and overstory variables. Ordination and indicator species analysis characterized geomorphic and other environmental gradients in amphibian assemblages and suggested spatial compression of fluvial habitats and riparian-associated species in zero-order basins, in comparison with downstream areas. Our findings have implications for headwater areas managed to hedge risk to and uncertainty in amphibian persistence, namely in the delineation of zones with species management priority, and in the maintenance of natural fluvial and hillslope disturbance regimes, along with the microhabitat features created by these regimes.

Résumé : Des bassins d'ordre zéro, s'étendant des lignes de crête jusqu'à l'origine des ruisseaux de premier ordre, ont été échantillonnés dans la chaîne côtière de l'Oregon pour (i) caractériser les patrons de répartition spatiale des espèces et des assemblages d'amphibiens le long de gradients longitudinaux et latéraux et en regard de trois entités géomorphologiques (vallées, sommets et versants); et (ii) développer des modèles empiriques espèces–habitats. Les bassins d'ordre zéro non aménagés étaient des points chauds pour la diversité des amphibiens, avec des différences significatives entre les gradients géomorphologiques. Les captures d'amphibiens associés au milieu riverain ont été plus nombreuses dans les vallées, habituellement à moins de 2 m du centre du bassin. Les amphibiens associés aux milieux non riverains ont été capturés deux fois plus loin du centre des bassins que les espèces riveraines, mais c'est seulement à 2–5 m du centre des bassins que leur densité était la plus forte. Les modèles empiriques les plus utiles sont ceux qui mettent en relation les espèces individuelles d'amphibiens avec les variables géomorphologiques, les perturbations, l'humidité et la voûte forestière. L'ordination et l'analyse d'espèces indicatrices ont fait ressortir des gradients d'assemblages d'amphibiens selon la géomorphologie et d'autres variables environnementales et elles montrent une compression spatiale des habitats fluviaux et des espèces riveraines dans les bassins d'ordre zéro en comparaison avec les milieux en aval. Nos résultats ont des implications en regard des têtes de bassins aménagées pour limiter le risque et l'incertitude entourant la persistance des amphibiens, allant de la délimitation de zones prioritaires d'aménagement d'espèces au maintien des régimes de perturbations naturelles des versants et des secteurs fluviaux, ainsi qu'aux caractéristiques des microhabitats créés par ces régimes.

[Traduit par la Rédaction]

Introduction

In western North America, headwater drainages make up a large proportion of the forested landscape (Hack and Goodlett 1960; Benda 1990; USDA and USDI 1994, Appendix V-G). Portions of the central Coast Range in Oregon have a drainage density of 2.9 km of streams/km² (USDI

2000). Because of their frequency and areal extent in mountainous forested landscapes, role in transport of materials down-gradient to higher-order systems (Benda 1990; May and Greswell 2003), and influence on downstream water quality (Forest Ecosystem Management Team 1993; Beschta et al. 1987), it is probable that small headwater drainages are important in the maintenance of ecosystem integrity, a com-

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Table 1. Comparison of riparian zone management practices in forested mountain streams of the Pacific Northwest (adapted from Young 2000), and amphibian species of concern in zero-order basins.

	Basin type		Zero-order	Species of concern ^a
	Perennial	Intermittent		
Government jurisdiction	>Second-order	First- and second-order		
British Columbia	20-m buffer; 20-m management zone	No buffer; 20-m management zone	None	Tailed frog, Pacific giant salamander
U.S. federal lands ^b	1–2 site-potential tree heights	1 site-potential tree height	Variable by slope and geology	Tailed frog, southern torrent salamander, Dunn's salamander, clouded salamander
Washington State and private	No buffer; 7.5–30 m management zone	None	None	Dunn's salamander
Oregon State and private	6-m buffer; 30-m management zone	6-m buffer; 15-m management zone	None	Tailed frog, southern torrent salamander, clouded salamander
California State and private	45-m management zone	15-m management zone	None	Tailed frog, southern torrent salamander

^aSpecies designated sensitive or threatened by provincial, state, or federal governments.

^bLands covered by the Northwest Forest Plan.

mon objective for forestry practices in the Pacific Northwest.

Biodiversity policies on U.S. federal lands necessitate maintenance and restoration of habitat to support well-distributed populations of native species within autonomous geophysical landscape units, such as riparian areas (Forest Ecosystem Management Team 1993). A significant component of ecosystem management in drainage basins in the Pacific Northwest has involved the installation of riparian buffers, areas where disturbance from forest management is reduced to minimize impact to riparian species. Buffers have traditionally been established based on stream size and fish usage (Belt and O'Laughlin 1994), extending some predetermined distance laterally from fluvial centers. Differences in management practices across landownerships in the Pacific Northwest (Gregory 1997), particularly in headwater areas (Table 1), have resulted in scrutiny of resources in headwater areas and in reassessment of ecological values warranting protection. For basins supporting ephemeral streams in particular, protection of native ecosystem resources is negligible in current management guidelines, while installation of downstream protections has left these headwater areas open to continued anthropogenic disturbances (Welsh 2000).

Ephemeral systems, also called zero-order basins, dominate the drainage area of most soil-mantled hillslopes (Hack and Goodlett 1960; Benda 1990; Kikuchi and Miura 1993). Zero-order basins are hillslope units where flow lines converge on a hollow (Tsukamoto et al. 1982), and they include catchment areas above sustained scour and deposition as well as intermittent scour areas. Zero-order basins extend from ridgelines down to the initiation of first-order streams and may include areas defined as hollows (Montgomery and Dietrich 1989; Benda 1990) and ephemeral or intermittent streams (USDA and USDI 1994). These basins have been studied for their unique physical characteristics, including their disturbance regimes (Reneau and Dietrich 1990; May and Greswell 2003) and moisture relations (Dietrich et al. 1987).

Although studies have characterized vertebrate (McComb et al. 1993) and plant (Pabst and Spies 1998; Nierenberg and

Hibbs 2000) presence in larger unmanaged headwater riparian drainages, few studies have characterized species assemblages in unmanaged zero-order basins (Waters et al. 2002). The upper limits of riparian species in drainage basins have not been well defined. Biotic patterns in larger headwater areas are organized by geomorphic and other abiotic processes (Kovalchik and Chitwood 1990; Hack and Goodlett 1960; Gregory et al. 1991; Pabst and Spies 1998). In particular, the spatial arrangement of amphibians in larger headwater drainages reflects shaping by these abiotic processes (e.g., Dupuis and Bunnell 2000; Wilkins and Peterson 2000; Waters et al. 2002). It is unclear whether the spatial patterning of amphibians in zero-order basins follows similar patterns.

Amphibian species may be key components of forest management in zero-order basins. Amphibians have relatively high biomass in headwater stream systems (Bury 1988; Vesely 1997) and have been proposed as environmental indicator species (Welsh and Olivier 1998; Welsh and Droegge 2001), owing, in part, to their associations with late-successional forests and sensitivity to management activities (Corn and Bury 1989; Welsh 1990; Blaustein et al. 1995). The low vagility and peripatry of many forest-associated amphibians lead to a tight coupling of densities to habitat elements commonly influenced by forest management, such as down wood volumes and overstory conditions (Corn and Bury 1989; Forest 1993).

Amphibian assemblages have been characterized in both managed (Vesely 1997; Wilkins and Peterson 2000; Olson et al. 2000; Stoddard 2001) and unmanaged (Bury et al. 1991; Welsh and Lind 2002; Welsh and Olivier 1998; Adams and Bury 2002) headwater streams. Preliminary results of Olson et al. (2000) showed changes in amphibian assemblages from aquatic and splash-zone species to species favoring drier habitat elements concomitant with changes in streams from perennial systems to channels "above water". However, Olson et al. (2000) did not consider unmanaged systems, and they did not clearly define species assemblages associated with zero-order basins and their geomorphic surfaces. Studies of amphibian fauna in unmanaged systems can pro-

vide a baseline for evaluating species composition and ecosystem integrity in contexts where disturbance may mask subtle environmental gradients (Adams and Bury 2002).

Our study examines the spatial arrangement and habitat associations of amphibians in unmanaged zero-order basins in the Oregon Coast Range. Specifically, we investigate (i) spatial distribution patterns of individual amphibian species along longitudinal and lateral gradients, and relative to three geomorphic surfaces (valleys, headmost areas, and slopes); (ii) amphibian species-specific associations with environmental variables; and (iii) composition of amphibian assemblages in zero-order basins, and their associations with environmental gradients. Finally, we discuss forest management implications of the resulting amphibian species – habitat relationships and amphibian assemblage compositions in zero-order basins.

Materials and methods

Study area

The study area was chosen based on landownership, the presence of large unmanaged areas, a relatively high density of first-order systems (over 13 first-order streams/km²), and similarities in landscape attributes, including vegetation, geology, elevation, and marine influence. Work was conducted on U.S. federal lands administered by the Coos Bay District of the Bureau of Land Management (BLM) in the central Oregon Coast Range (Fig. 1). The study area encompassed approximately 850 km² of the headwaters of the Coquille River basin (4767N to 4798N, 418E to 445E Universal Transverse Mercator). The area is underlain by uplifted sea floor sediment and basalt, with geologic formations composed of sandstone and sandy siltstone (USDI 2000). Soils in study sites included principally series in the Preacher–Bohannon and Umpcoos – Rock Outcrop units. Within the Coast Range physiographic province, maximum air temperatures seldom exceed 30°C, and minimum air temperatures rarely fall below freezing (USDI 2000). Most precipitation occurs as rainfall, ranging from 1397 to over 3810 mm annually (Oregon State University Extension Service 1982). The area is deeply dissected by stream networks and has a drainage density of 2.9 km of streams/km², ca. 76% of which are first- and second-order systems (USDI 2000).

This area is in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone (Franklin and Dyrness 1973). Forested upland areas are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock. Forest floor species include evergreen huckleberry (*Vaccinium ovatum* Pursh), salal (*Gaultheria shallon* Pursh), sword fern (*Polystichum munitum* (Kaulf.) Presl), and oxalis (*Oxalis oregana* Nutt.). Riparian areas support principally hardwood overstory trees including red alder (*Alnus rubra* Bong.). Riparian terrace species include salmonberry (*Rubus spectabilis* Pursh) and stinking black currant (*Ribes bracteosum* Dougl.).

Study sites

A set of criteria was applied a priori to all zero-order basins within the study area to identify suitable sites. Sites disturbed by management activities, sites >0.8 km from a transportation corridor, and zero-order basins that did not

contribute to the initiation of a first-order channel (Dietrich et al. 1987) were eliminated. Using geographic information system maps of landownership, stand ages, roads, first-order streams, and contour crenulations (produced by 10-m digital elevation models), we identified 222 zero-order basins fitting these criteria. Preliminary observations suggested that zero-order basin habitat variables varied with differences in slope and aspect. We therefore stratified zero-order basins into high ($\geq 39^\circ$) and low ($< 39^\circ$) slope classes, and into south- and west-facing ($120\text{--}300^\circ$) and north- and east-facing ($301\text{--}119^\circ$) aspect classes. All 222 systems were numbered, and a random-number generator was used to determine the order of sites visited, alternating by slope and aspect class. The sample population includes the first 63 randomly selected zero-order basins from the inference population of 222 zero-order basins.

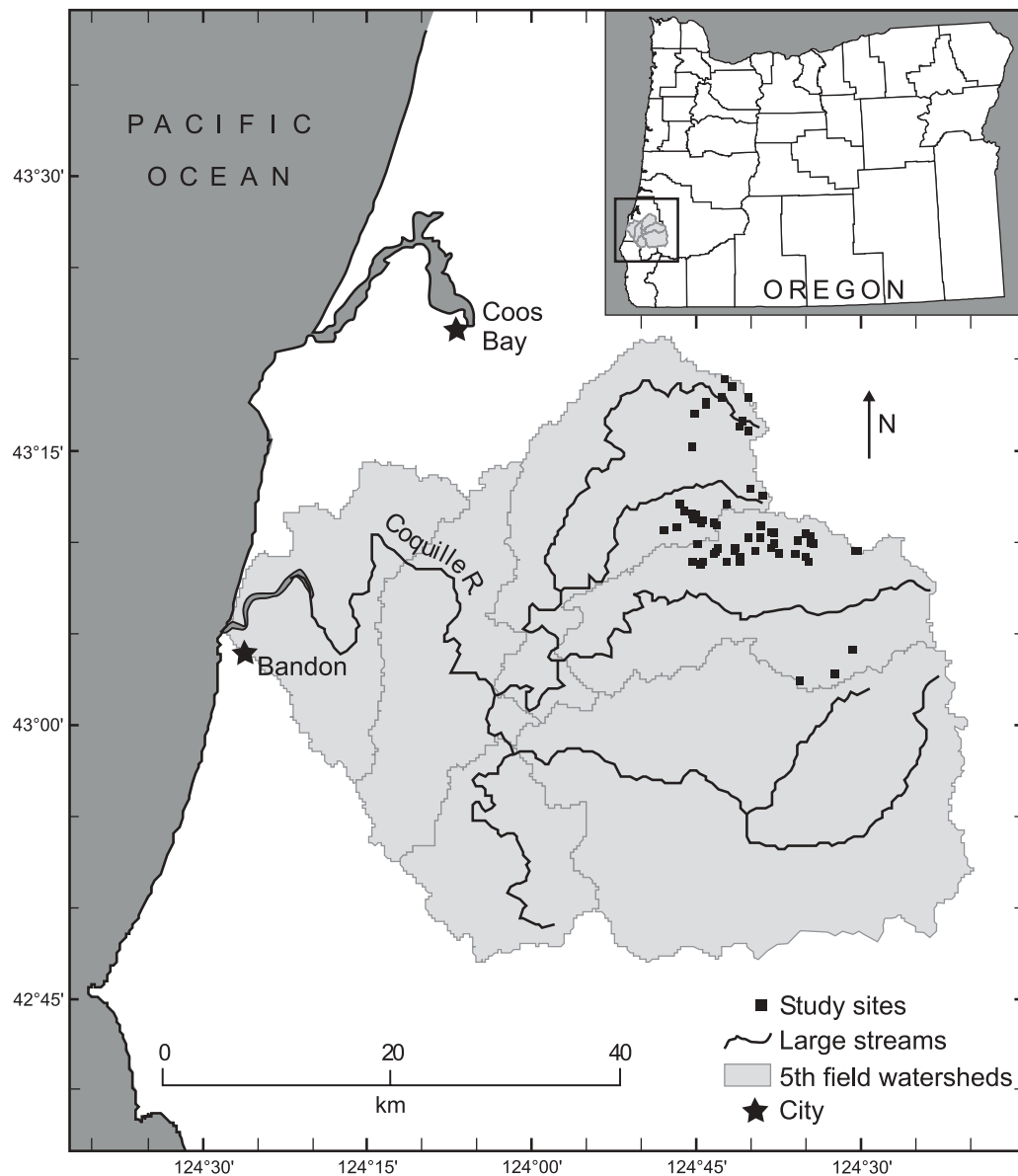
Data collection

In the field, we delineated the extent of each zero-order basin as the area extending downslope from the ridgeline to the point where fluvial scour became clearly more continuous than discontinuous (estimated visually over a channel length of 15 m), often at the junction with another zero-order basin. Within delineated zero-order basins, we established a longitudinal axis along and parallel to the most fluvially active portion of the basin (Fig. 2). We considered this longitudinal axis to be the basin center. Measurements of distance from ridge to sampling transect were measured along this axis. Lateral measurements of distance from basin center were measured perpendicular to this axis (Fig. 2, detail area).

Several authors have suggested that community patterns and biological diversity in headwater streams are organized along geomorphic gradients (Hack and Goodlet 1960; Gregory et al. 1991; Pabst and Spies 1998). Within zero-order basins we delineated three geomorphic surfaces: valleys, headmost areas, and slopes (Fig. 2). We defined valley geomorphic surfaces as convergent areas below (downstream of) the first evidence of scour and deposition. We defined headmost areas as convergent, filled valley areas above the first evidence of scour and deposition, extending upslope to a topographic break. Headmost areas were inclusive of both hollows and source areas, as defined by Montgomery and Dietrich (1989). We defined slope geomorphic surfaces as nonconvergent, planar surfaces, extending laterally from valley floors to ridgelines.

We established six amphibian sampling transects within each zero-order basin, two in each geomorphic surface (Fig. 2). Transects in valley and headmost surfaces included a 15 × 4 m section centered on the basin center and extending upstream along the longitudinal axis, and a 5 × 4 m section established perpendicular to the longitudinal axis, overlapping the upstream end of the longitudinal transect by 4 m². The total survey area within each of these amphibian transects was 76 m². This “L-shaped” transect design was chosen to compare amphibian densities in valley surfaces with densities in lower slope geomorphic surfaces (“transition” slopes, as defined in Pabst and Spies 1998). Transects within slope geomorphic surfaces were placed perpendicular to the first and final in-valley transects, on opposite sides of the basin. Each slope transect consisted of one 15 × 4 m sec-

Fig. 1. Location of the study area and the 63 study sites within the Coquille Basin, southwestern Oregon.



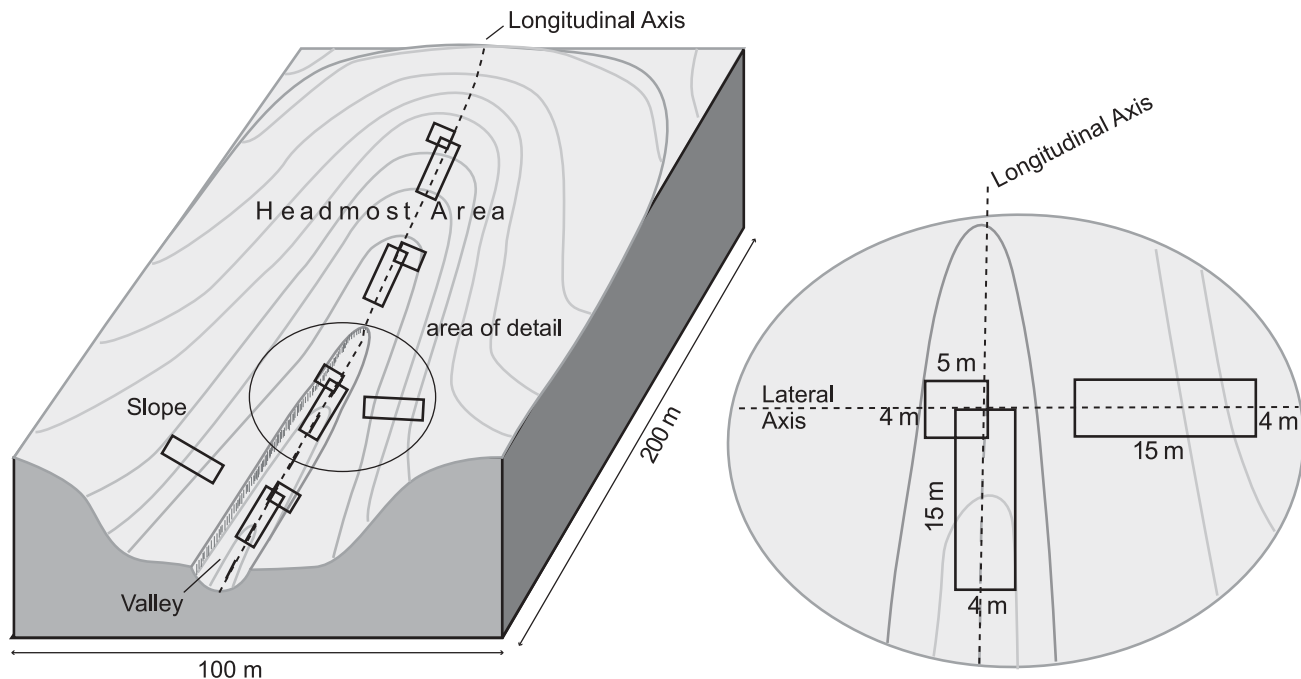
tion (60 m²). Where the lateral distance from basin center to ridgeline was >30 m, the start point of slope transects was established halfway between basin center and ridgelines, perpendicular to the longitudinal axis. Where total slope length was <30 m, the start points of slope transects were placed 5.0 m from basin center.

We surveyed for amphibians from March through June in 2000 and 2001. Amphibians were sampled once per basin. We sampled amphibians in each transect using time-constrained searches of all cover objects and litter (Bury and Corn 1991) for a maximum of 30 min, not including animal processing time. All cover objects were removed and litter was combed systematically, from the downstream end of transects. If 30 min elapsed before we could search all cover objects in a transect, the searched area was reduced and recorded accordingly.

We measured 31 environmental variables (Table 2) that may be important in structuring amphibian assemblages

within zero-order basins. These data were collected at plot, transect, and zero-order basin spatial scales. Plots were established within geomorphic surfaces within basins, following a stratified random design described in Sheridan (2002). Plots were 2 m² in size, and 17 were placed in each basin. At the plot scale, data were collected for three substrate, two down wood, and nine overstory variables. Binary variables for the presence-absence of saturation, scour, deposition, and stability in individual plots became proportions when averaged for geomorphic surfaces. Overstory variables were measured using variable-radius sampling in one plot per geomorphic surface. At the amphibian transect scale, data were collected on two positional, one surface moisture, and four scour and deposition variables. At the zero-order basin level, we collected data on geomorphic surface, basin gradient, basin depth, heat load index (a cosine transformation of basin aspect), and flow area above the initiation of scour and deposition. Data collected on covariates were date of survey,

Fig. 2. Schematic of geomorphic surfaces and amphibian transect set up within zero-order basins.



relative humidity, temperature, stand age, and distance from ocean.

Statistical analyses

Spatial distribution patterns

We used several analyses to examine longitudinal and lateral distribution patterns of amphibians. First, between species, we compared proximity to ridgeline to determine the relative longitudinal extent of amphibians in zero-order basins. We considered the shortest slope distance along the longitudinal axis from ridgeline to a species capture in a zero-order basin as that species' proximity to ridgeline. We made between-species comparisons of proximity to ridgeline, using a general linear model (PROC GLM, SAS Institute Inc. 1999) with \log_{10} of proximity to ridgeline as the response variable and species as the explanatory variable. We estimated the size of differences in first detection between species using pairwise means comparisons with a Tukey-Kramer adjustment to account for the large number of unplanned comparisons (Ramsey and Schafer 1997).

Similarly, we contrasted species' use of areas along lateral axes using between-species comparisons of maximum distance from basin center for each zero-order basin. We analyzed differences using a general linear model with the \log_{10} of maximum distance from basin center to capture as the response variable and species as the explanatory variable. We estimated the size of differences in lateral extent between species using pairwise means comparisons with a Tukey-Kramer adjustment for unplanned comparisons.

Within species, we compared differences in captures between lateral zones to examine species-specific penetration of "dry" and "moist" habitats. We estimated differences in amphibian capture rates associated with lateral distance from basin center, using log-linear regression models (PROC GENMOD, SAS Institute Inc. 1999), because amphibian

species captures were collected as count data. For this analysis we summed species captures for each of three lateral zones: 0–2, 2–5, and >5 m (slope transect data) from basin center. Lateral zone was the explanatory variable and captures was the response variable for each model, for each species. We used a compound symmetry model (SAS Institute Inc. 1999), which assumes constant variance and covariance, to model spatial autocorrelation between lateral zones within zero-order basins. We included an offset to account for different sampling effort between lateral zones.

Geomorphic surfaces integrate longitudinal and lateral environmental gradients in zero-order basins, and we hypothesized that species' densities would differ between geomorphic surfaces. Within species, we estimated differences in captures between geomorphic surfaces using log-linear regression models (PROC GENMOD, SAS Institute Inc. 1999). For this analysis, we summed transect capture data for each geomorphic surface (valley, headmost, and slope) in each zero-order basin. Geomorphic surface was the explanatory variable and number of captures per geomorphic surface was the response variable, for each species. As in within-species lateral analyses, we used a compound symmetry correlation structure to model spatial autocorrelation between geomorphic surfaces within a zero-order basin and included an offset to account for different sampling effort. For both lateral zone and geomorphic surface models, we assessed goodness of fit using estimated deviance/degrees of freedom (df), examination of residuals for outliers, and comparison of model predicted values with actual values.

Amphibian associations with environmental variables

We developed sets of empirical log-linear regression models (PROC GENMOD, SAS Institute Inc. 1999) describing amphibian capture rates in unmanaged zero-order basins as a function of geomorphic, surface moisture, substrate, canopy cover, down wood, and overstory variables. We con-

Table 2. Description of habitat parameters collected at the plot, transect, or zero-order-basin scale, covariates, parameter codes (used in empirical models), references for importance of ecological variables, and species hypothesized to be associated with variables.

Parameter	Code	Description	References ^a	Species ^b
Plot scale				
Large substrate (%)	LRGSUB	Visual estimate of % plot surface obscured by gravel, cobble, boulders, or bedrock (substrates >5 mm)	Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander (-), ensatina (-)
Organic substrate (%)	ORGSUB	Visual estimate of % plot surface obscured by litter, organic material, bark, or down wood	Corn and Bury 1991; Blaustein et al. 1995	Western red-backed salamander, clouded salamander (-), ensatina
Litter depth (cm)	LITTER	Litter depth averaged from five points/plot	Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander (-), Dunn's salamander (-), western red-backed salamander (-), clouded salamander (-), ensatina
Transect scale				
Ridge distance (m)	DISTRIDG	Ridgeline to plot slope distance, divided by distance from ridgeline to initiation of scour		Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander (-), ensatina (-)
Distance from center (m)	DISTC	Perpendicular slope distance from basin center to plot location	Leonard et al. 1993; Blaustein et al. 1995; Vesely 1997; Bury et al. 1991	Western red-backed salamander (-), clouded salamander, ensatina
Surface moisture	MOISTR	Integer index of plot moisture based on categories described in Olson et al. 1999; values range from 1 (dry) to 7 (flowing)	Bury et al. 1991	Southern torrent salamander, western red-backed salamander
Saturation	SATUR	Presence-absence of field-estimated "saturated" conditions	Bury et al. 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander (-), ensatina (-)
Scour	SCOUR	Presence-absence of scour (removal of above-ground vegetation and litter)	Bury et al. 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander
Deposition	DEPOSIT	Presence-absence of deposition (material from outside of the plot mobilized by fluvial or hillslope disturbance)		Southern torrent salamander, Dunn's salamander, western red-backed salamander
Stability	STABLE	Presence-absence of stable conditions (no scour or deposition)		Western red-backed salamander (-), clouded salamander (-), ensatina
Down wood volume (m ³ /ha)	CWDM3HA	Volume of down wood, calculated from visually estimated down wood	Leonard et al. 1993; Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, ensatina
Down wood frequency	WOODFREQ	Presence-absence of down wood	Leonard et al. 1993; Blaustein et al. 1995; Corn and Bury 1991	Clouded salamander
Canopy cover (%)	CCTOT	% of view screen obscured in a canopy viewer (Mueller-Dombois and Ellenburg 1974)	Corn and Bury 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, ensatina
Large overstory (m ² /ha)	BA70	Basal area of trees over 70 cm in diameter	Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, ensatina

Table 2 (continued).

Parameter	Code	Description	References ^a	Species ^b
Relative density	RD	Tree density metric calculated from basal area and quadratic mean diameter (Curtis 1982), using basal area from variable-radius overstory plots and visually estimated diameters	Vesely 1997	Western red-backed salamander
Relative density within geomorphic surfaces	RDIN	Relative density (similar to Curtis 1982), calculated using only trees rooted in the same geomorphic surface as the variable-radius plot		Southern torrent salamander (-), Dunn's salamander (-), western red-backed salamander, clouded salamander, ensatina
Relative density of hemlock	RDSHE	Relative density (similar to Curtis 1982), calculated using only western hemlock trees in variable-radius overstory plots		Southern torrent salamander (-), Dunn's salamander (-), western red-backed salamander, clouded salamander, ensatina
Relative density of hardwoods	RDHW	Relative density (similar to Curtis 1982), calculated using only hardwood species in variable-radius overstory plots		Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander (-), ensatina (-)
Snag density (no./ha)	SNAGS	Snags per hectare, calculated from variable-radius overstory plots	Corn and Bury 1991	Clouded salamander
Fern cover (%)	FERNS	% plot surface obscured by ferns	Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander, Dunn's salamander, clouded salamander
Shrub cover	SHRUBS	% plot surface obscured by shrubs	Vesely 1997	Southern torrent salamander (-), Dunn's salamander (-), western red-backed salamander, clouded salamander (-)
Zero-order-basin scale				
Geomorphic surface	GEOSRF	Three classes: valley, headmost area, and slope		Western red-backed salamander, clouded salamander, ensatina
Basin gradient (degrees)	GRADE	Gradient (slope) of zero-order basin, calculated using difference in elevation and measured length of basin	Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, ensatina
Feature depth (m)	DEPTH	Difference in elevation between the midpoint of the geomorphic surface and the surrounding ridgeline		Southern torrent salamander, Dunn's salamander, ensatina (-)
Heat load index	HEATNDX	Relative measure of solar gain, calculated using the formula: $1 - \cos(\text{aspect}-45)/2$ (Beers et al. 1966); 0 represents cool (45°) aspects, 1.0 represents warm (225°) aspects	Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander (-), Dunn's salamander (-), western red-backed salamander, clouded salamander (-), ensatina (-)
Basin area (ha)	AREA	Area potentially contributing surface flow to the point of initiation of scour and deposition in a zero-order basin; generated in ARC/INFO, using flow direction and accumulation algorithms and a 10-m digital elevation model		Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander (-), ensatina (-)
Covariates				
Day number	DAY	Number of days from January 1 to survey date		Southern torrent salamander (-), Dunn's salamander (-), western red-backed salamander, clouded salamander (-), ensatina (-)

Table 2 (concluded).

Parameter	Code	Description	References ^a	Species ^b
Relative humidity (%)	RH	Relative humidity of transect area (sling psychrometer)		Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, ensatina
Temperature (°F)	TEMPF	Air temperature in transect area during survey		Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, ensatina
Elevation (m)	ELEV	Zero-order basin ridge elevation (altimeter)	Bury et al. 1991	Southern torrent salamander (–), Dunn's salamander (–), western red-backed salamander (–), clouded salamander (–), ensatina (–)
Ocean distance (km)	DISTOCN	Distance from ocean, derived from ARC/INFO GIS coverages of the study area		Southern torrent salamander (–), Dunn's salamander (–), western red-backed salamander (–), clouded salamander (–), ensatina (–)
Stand age (years)	AGE	Stand age of forested areas in the zero-order basin, derived from ARC/INFO GIS coverages of the study area	Blaustein et al. 1995; Corn and Bury 1991	Southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, ensatina

^aKey literature suggesting that the parameter may be related to amphibian density.

^bSpecies for which the parameter was used in habitat-association models. A negative sign in parentheses next to the species indicates that the parameter had a hypothesized negative effect on species capture.

sidered amphibian species with >50 captures as having large enough numbers to be informative. For this analysis, amphibian captures were summed for each geomorphic surface in each zero-order basin. Environmental variables collected at the plot and transect level were averaged for each geomorphic surface, and basin-level variables were applied to all geomorphic surfaces they contained. We addressed spatial autocorrelation between geomorphic surfaces using generalized estimating equations (PROC GENMOD, SAS Institute Inc. 1999) and included an offset in models to account for different sampling effort in different geomorphic surfaces.

We used an information-theoretic approach to development and selection of species-habitat models (Burnham and Anderson 1998), based on careful a priori development of models and inference based on model likelihood. We developed a priori hypotheses about relationships between amphibian densities and habitat conditions based on existing literature (Table 2) and from general ecological theories (e.g., microclimate concepts (canopy cover, feature depth), island biogeography concepts (basin area, large overstory)). We then expressed these competing hypotheses as statistical models and fit the models to amphibian capture data for each species (Appendix A). We constrained the number of variables to a maximum of five per model (excluding intercept), to allow tractability and the ability to discern among different processes. We used a log_e transformation for variables hypothesized to have a threshold effect (sensu Franklin et al. 2000) on amphibian captures (e.g., wood volume). Where Spearman's rank correlations between variables were >0.6 within a model, we subjectively eliminated correlated variables. Because ecological models were not hierarchically nested (Burnham and Anderson 2001), we developed a single global model containing the majority of the uncorrelated variables used in each model set to assess model fit and overdispersion for the model set. A null model, with only an intercept and no explanatory variables, was included to determine whether any of the explanatory variables gave a better fit to the response variable (amphibian captures) than consideration of the response mean alone.

For each model set, we used Akaike's Information Criterion (AIC), an estimate of the loss of information when a model is used to approximate truth, for both model ranking and parameter estimation (Burnham and Anderson 1998). AIC selection methods are based on model parsimony and penalize over-parameterized models.

For model selection and ranking, we first calculated QAICc, a more precise version of AIC adjusting for small sample size and incorporating quasi-likelihood modifications (Burnham and Anderson 1998). The model with the smallest QAICc value (highest likelihood) was selected as the best approximation for the information in the data, relative to the models considered. Models within 2 QAICc units of the best approximating model ($\Delta\text{QAICc} \leq 2$) were considered to represent reasonable competing hypotheses (Burnham and Anderson 1998). These best models were investigated for goodness of fit by evaluating model deviance/df, by comparing the best models with the rank of the null model, and by comparing the predicted values with observed data. The strength of evidence for other models in each set was ranked relative to the best model, using ΔQAICc , the difference be-

tween the QAICc value for a given model and the model with the lowest QAICc value in the set. ΔQAICc values were used to compute Akaike weights (w), estimates of the relative likelihood of each model, given the likelihood of the full set of candidate models (Burnham and Anderson 2001).

We investigated the relationship between amphibian capture rates and individual environmental variables using adjusted confidence intervals and parameter predictor weights. For models with $\Delta\text{QAICc} \leq 2$, we developed estimates of the unconditional sampling variation of model variables and used it to adjust 95% confidence intervals for model variables (Burnham and Anderson 1998). We only interpreted adjusted confidence intervals for variables that had consistent and strong relationships with amphibian captures in the best models (models with $\Delta\text{QAICc} \leq 2$). We compared the relative importance of variables in each model set by computing parameter predictor weights (Burnham and Anderson 2001), an indicator of the importance of individual variables in predicting response, considering the entire model set. Predictor weights were calculated by summing the adjusted Akaike weights (w) for all the models in which a parameter occurred. Akaike model weights (w) were adjusted following Stoddard (2001), using the formula:

$$\begin{aligned} \text{adj. } w &= (\text{no. models/no. models with the variable}) \\ &\quad \times (1/\text{no. variables}) \times w \end{aligned}$$

This adjustment was made to account for large differences in the numbers of models associated with individual variables.

Composition of amphibian assemblages

We examined the compositions of amphibian assemblages in zero-order basins and their relationships to environmental gradients using nonmetric multidimensional scaling (NMS) and indicator species analysis. We used NMS (May 1976), an ordination technique in PC-ORD (McCune and Mefford 1999), to depict relationships between experimental units (geomorphic surfaces), in terms of amphibian composition. We used a Sorenson distance measure (McCune and Grace 2002) and detrended correspondence analysis (Hill and Gauch 1980) to establish starting coordinates for the ordination. Interpretation of ordination axes was facilitated by consideration of Spearman's rank correlations between environmental variables and axis scores. The final ordination was rotated to maximize correlations between axis 1 and the environmental variable with the single highest correlation with the ordination space. Ellipses were drawn around areas in ordination space with the highest density of each species.

We used indicator species analysis (Dufrene and Legendre 1997) to characterize amphibian assemblages associated with both geomorphic surfaces and lateral zones in zero-order basins. This analysis compared species abundance and consistency in individual geomorphic surfaces or lateral zones with their abundance and consistency in all surfaces or zones to provide an indicator value. Indicator values represented the percentage of perfect indication of a species for a particular surface or zone, with 100% representing perfect indication (a species always being associated with that surface or zone, in relatively high numbers). Maximum indicator values represented the indicator value of a species for the

surface or zone with which it was most strongly associated. We developed amphibian assemblages associated with each geomorphic surface and lateral zone, considering only species whose maximum indicator values were significantly higher than values from Monte Carlo simulations (2000 iterations, $\alpha = 0.05$).

We compared the effectiveness of geomorphic surfaces and lateral zones in explaining amphibian species distributions using three techniques. We compared the total number of significant indicator species associated with each geomorphic surface and lateral zone. We used the sum of all species indicator values for each surface or zone as an additional criterion to compare geomorphic surfaces and lateral zones for their ability to explain species distributions (Dufrene and Legendre 1997). Finally, we used a multi-response permutation procedure (MRPP, Biondini et al. 1988) to test the hypothesis of no difference between individual geomorphic surfaces and between individual lateral zones. We used MRPP in PC-ORD (McCune and Mefford 1999) with Sorenson distance and rank transformation of the distance matrix to address loss of sensitivity due to community heterogeneity. We estimated effect size using chance-corrected within-group agreement (A) as an estimate of within-group homogeneity compared with random expectation.

Results

We surveyed 382 transects in 63 unmanaged zero-order basins and captured a total of 865 amphibians belonging to eight species (Table 3): western red-backed salamander (*Plethodon vehiculum* (Cooper)), southern torrent salamander (*Rhyacotriton variegatus* Stebbins and Lowe), Dunn's salamander (*Plethodon dunni* Bishop), clouded salamander (*Aneides ferreus* Strauch), ensatina (*Ensatina eschscholtzii* Gray), Pacific giant salamander (*Dicamptodon tenebrosus* Good), tailed frog (*Ascaphus truei* Stejneger), and northwestern salamander (*Ambystoma gracile* (Baird)). Only terrestrial (adult) forms of tailed frog and northwestern salamander were observed. Adult and juvenile forms of other species were encountered, including both terrestrial and aquatic forms of the Pacific giant salamander. Four of the eight amphibian species identified have a status of concern in all or parts of their ranges (Table 1). Captures averaged over 6.3 detections/surveyor-hour (95% CI, 5.48–7.26). Amphibian densities were highly variable by species and geomorphic surface (Table 3). Mean amphibian diversity (Shannon index, H') in zero-order basins was low (range, 0–1.77) and varied by geomorphic surface (Table 3). Amphibian diversity in valley geomorphic surfaces was 0.33 units higher (95% CI, 0.16–0.50) than that in headmost surfaces. Amphibian diversity in headmost areas was 0.13 units higher than that in slope areas. This trend was not statistically significant (95% CI, –0.05 to 0.30), but may be important biologically, as the amphibian fauna of headmost areas appeared distinct from that of slope and surrounding upland areas.

Amphibian abundances in zero-order basins restricted their use in analyses. Pacific giant salamander, southern torrent salamander, Dunn's salamander, western red-backed salamander, clouded salamander, and ensatina were used in

Table 3. Herpetofauna detected in unmanaged zero-order basins: number of captures, density (for species with over 30 captures), total richness, and diversity (mean of the Shannon index, H') for each geomorphic surface, as well as spatial metrics, including proximity to ridgeline and distance from basin center, for species with over 30 captures.

Species	Geomorphic surface						Spatial metrics		
	Valley, $n = 63$			Headmost, $n = 63$			Slope, $n = 63$		
	No. of captures	Density (captures/1000 m ²)	No. of captures	Density (captures/1000 m ²)	No. of captures	Density (captures/1000 m ²)	Total captures	Proximity to ridgeline, $n = 12-52$ (m) ^d	Distance from basin center, $n = 12-52$ (m) ^d
Western red-backed salamander	88	9.31 (6.65–11.97)	101	11.14 (7.85–14.44)	92	12.36 (9.45–15.28)	281	139.40 (109.00–169.80)	21.27 (16.98–25.56)
Southern torrent salamander	139	16.06 (10.63–21.5)	27	2.35 (0.43–4.27)	2	0.3 (–0.12 to 0.72)	168	174.60 (139.20–209.99)	1.89 (–0.06 to 3.84)
Dunn's salamander	121	12.85 (9.48–16.22)	34	3.13 (1.46–4.81)	5	0.61 (0.08–1.14)	160	170.71 (142.90–198.53)	3.40 (1.81–5.00)
Clouded salamander	28	2.8 (1.66–3.95)	64	8.83 (5.64–12.02)	37	4.75 (2.84–6.66)	129	112.09 (91.63–132.55)	14.28 (9.85–18.72)
Ensatina	5	0.38 (–0.01 to 0.78)	40	5.68 (3.36–8.01)	32	3.93 (2.23–5.63)	77	104.53 (81.81–127.24)	14.86 (9.71–20.00)
Pacific giant salamander	32	3.17 (1.68–4.66)	2	0.28 (–0.11 to 0.67)	1	0.11 (–0.10 to 0.33)	35	174.5 (137.53–211.47)	0.38 (–0.26 to 1.01)
Tailed frog	5		1		1		7		
Plethodontid juveniles (<15 mm)	7		0		0		7		
Northwestern salamander	0		1		0		1		
Southern alligator lizard	0		1		0		1		
Total captures	425		270		170		865		
No. of transects	136		119				127		
Richness	7		8				7		
Diversity (H')	0.89 (0.76–1.01)		0.56 (0.42–0.69)				0.49 (0.31–0.55)		

Note: Values in parentheses are 95% confidence intervals.
^dSample sizes (n) for spatial metrics are variable, depending on species' presence in zero-order basins.

Table 4. Between-species comparisons of longitudinal and lateral spatial extents in zero-order basins.

Species 1	Species 2	Proximity to ridgeline	Distance from center
Pacific giant (A)	Ensatina	1.92 (1.02–3.63)*	0.17 (0.06–0.42)*
	Clouded	1.75 (0.93–3.23)	0.17 (0.07–0.43)*
	Western red-backed	1.59 (0.87–2.91)	0.1 (0.04–0.23)*
	Dunn's	1.11 (0.6–2.04)	0.47 (0.19–1.15)
	Pacific giant (T)	1.11 (0.5–2.47)	0.41 (0.11–1.54)
	Southern torrent	1.1 (0.59–2.05)	1.88 (0.59–5.97)
Pacific giant (T)	Ensatina	1.73 (0.9–3.33)	0.41 (0.13–1.31)
	Clouded	1.56 (0.82–2.94)	0.42 (0.13–1.33)
	Western red-backed	1.43 (0.76–2.67)	0.24 (0.08–0.73)*
Southern torrent	Ensatina	1.75 (1.14–2.7)*	0.22 (0.11–0.43)*
	Clouded	1.59 (1.05–2.38)*	0.23 (0.12–0.43)*
	Western red-backed	1.45 (0.98–2.13)	0.13 (0.07–0.23)*
	Pacific giant (T)	1.02 (0.53–1.96)	0.53 (0.17–1.70)
	Dunn's	1.01 (0.68–1.52)	0.61 (0.33–1.13)
Dunn's	Ensatina	1.72 (1.15–2.63)*	0.36 (0.19–0.68)*
	Clouded	1.56 (1.06–2.33)*	0.37 (0.20–0.68)*
	Western red-backed	1.44 (0.99–2.07)	0.21 (0.12–0.36)*
	Pacific giant (T)	1.01 (0.53–1.89)	0.87 (0.28–2.70)
Western red-backed	Ensatina	1.2 (0.81–1.82)	1.72 (0.93–3.23)
	Clouded	1.1 (0.75–1.61)	1.79 (0.99–3.23)
Clouded	Ensatina	1.1 (0.72–1.69)	0.97 (0.50–1.87)

Note: Values are ratios of median proximity to ridgeline and median maximum distance from center (with 95% CI in parentheses) for individual two-species comparisons made using general linear models with Tukey–Kramer adjustments to account for multiple comparisons. Results are ordered by size of proximity to ridgeline ratio. Asterisks indicates significant contrasts ($p \leq 0.05$). A, aquatic life form; T, terrestrial life form. Sample size (n) is 63.

comparisons of proximity to ridgeline and distance from basin center, as well as in ordination (NMS). Five of these species, all except Pacific giant salamander, were used in tests of differences in capture rates between geomorphic surfaces and between lateral zones, as well as in log–linear modeling. Indicator species analysis used all amphibians captured except northwestern salamander.

Spatial distribution patterns

There were differences between amphibian species in their highest (most upstream) detection and in their maximum distance from basin center (Table 4). The median distances to the most upstream detections of aquatic Pacific giant, southern torrent, and Dunn's salamanders were between 1.5 and 1.9 times further from ridgeline than those of clouded salamander and ensatina. The median maximum distances from basin center for Pacific giant, torrent, and Dunn's salamanders were less than half those of ensatina, clouded, and western red-backed salamanders. Other between-species comparisons were not significant.

There were also strong differences in capture rates of individual amphibian species between both lateral zones and geomorphic surfaces (Table 5). Torrent and Dunn's salamander captures were higher in areas within 5 m of basin center, with torrent salamander occurring almost exclusively within 2 m of center. Western red-backed and clouded salamanders were captured most frequently in areas 2–5 m from basin center. Capture rates of ensatina in the three lateral zones were similar. Median capture rates for torrent and Dunn's

salamanders were over three times higher in valleys than in headmost areas, and over six times higher in headmost areas than in slopes (Table 5). Clouded salamander and ensatina captures were significantly higher in headmost areas than in valleys, with ensatina occurring only very rarely in valley surfaces. There was a trend of more clouded salamander and ensatina captures in headmost areas than in slopes. Western red-backed salamander captures were similar across geomorphic surfaces. Estimates of deviance/df and graphs of residuals and observed versus predicted values suggested an acceptable fit for most models. Fit for the torrent salamander geomorphic surface model was poor; however, the direction and scale of the relationship appeared consistent with field observations and the natural history of this species.

Amphibian associations with environmental variables

Log–linear models of amphibian capture rates as a function of sets of environmental variables were developed for the five species with >50 captures. The number of models ranged from 28 models for southern torrent salamander to 30 models for western red-backed and clouded salamanders, including the global model, a null model, and five covariate models (Appendix A, Tables A1–A5). Spatial autocorrelation between geomorphic surfaces was relatively low (0.02 to 0.17). The scale parameter (a measure of overdispersion) and graphs of residuals and predicted versus observed values indicated moderately good fit of global models for each species. Best models ($\Delta\text{QAICc} \leq 2$) for each species are described below and presented in Table 6.

Table 5. Within-species ratios of median capture numbers (with 95% CI in parentheses) between lateral zones and between geomorphic surfaces in zero-order basins.

Species	Lateral zone contrasts			Geomorphic surface contrasts		
	Dev/df	Ratios		Dev/df	Ratios	
		0–2 m/2–5 m	2–5 m/>5 m		Valley/headmost	Headmost/slope
Southern torrent salamander ^a	1.36	6.08 (2.58–14.34)*	13.77 (1.63–116.27)*	1.80	4.95 (2.20–11.13)*	11.65 (2.36–57.55)*
Dunn’s salamander	1.07	1.52 (0.92–2.53)	9.09 (3.26–25.36)*	1.25	3.10 (1.75–5.49)*	6.12 (2.12–17.03)*
Western red-backed salamander ^b	1.56	0.49 (0.37–0.65)*	1.55 (1.10–2.17)*	1.69	0.78 (0.54–1.13)	0.96 (0.70–1.32)
Clouded salamander	1.44	0.53 (0.27–0.85)*	2.10 (1.02–3.45)*	1.38	0.38 (0.26–0.55)*	1.60 (0.95–2.72)
Ensatina	1.06	1.19 (0.30–1.45)	1.53 (0.39–1.79)	1.02	0.10 (0.03–0.30)*	1.16 (0.71–1.90)

Note: Asterisks indicate ratios significantly greater than 1.0 ($p \leq 0.05$); $n = 189$ (63 basins \times 3 lateral zones). Deviance divided by degrees of freedom (Dev/df) is provided as a model fit statistic.

^aThe lateral model included year (2000, 2001) as a covariate. The geomorphic model included day number as a covariate.

^bThe lateral model included day number as a covariate.

Southern torrent salamander

A priori models developed for southern torrent salamander reflected hypotheses that captures would be related to the presence of seeps, saturated conditions, larger substrate (gravels, talus), and shading (Appendix A, Table A1). For torrent salamanders, we modeled only valley and headmost areas, because only two captures occurred in slopes. The best approximating model (RV18) represented the hypothesis that torrent salamander captures in zero-order basins were influenced by basin gradient, heat load index, distance from ridge (corrected for distance from ridge to scour initiation), and saturation (Table 6). The Akaike weight of this model was 0.84; competing models had $\Delta\text{QAICc} > 5$, suggesting that they poorly approximated the data. The global model was initially ranked above all other models, because of a very high number of variables. This model was not consistent with analysis goals and was eliminated from consideration. The null model was ranked 26th out of the remaining 27 models ($\Delta\text{QAICc} = 176.19$), suggesting that torrent salamander captures were strongly related to some explanatory variables. However, the best model had moderately high deviance/df and only moderate fit of predicted to observed values, suggesting that although there was strong support for the best model in the a priori set, its usefulness as a descriptor of torrent salamander captures may be limited.

Normalized parameter predictor weights (Table 7) suggested that a positive effect of basin gradient and a negative effect of heat load index were the variables most strongly associated with torrent salamander captures in the full model set. The saturation variable occurred in all models within the 0.99 confidence set of cumulative model weights (Burnham and Anderson 2001), suggesting that saturation was also important. In the best model (RV18), a change from dry to saturated conditions resulted in a 51.3-fold (95% CI, 24.14–108.89) increase in median number of captures, holding other factors constant. Similarly, an increase in basin gradient of 1° was associated with a 2.4% (95% CI, 0.24–4.7) increase in captures.

Dunn’s salamander

The model set for Dunn’s salamander represented hypotheses that Dunn’s salamander captures were directly or indirectly linked to saturation, large substrate, and vegetative

shading (Appendix A, Table A2). Only valley and headmost zones were modeled, because only five captures occurred in slope zones. QAICc selected model PD11 as the single best approximating model, with no close competitors (Table 6). This model included variables for shrub cover, canopy cover, saturation, and large substrate. The best model had an Akaike weight >0.9 and was 18 times more likely than its closest competitor to be chosen as the best model in the set. The null model was ranked 25th out of 29 models ($\Delta\text{QAICc} = 62.64$), suggesting that variables in the best model were important in describing captures. Model PD11 had deviance/df of 1.3, with a moderately strong relationship between model predictions and observed values, suggesting a useful model fit.

Normalized parameter predictor weights supported a positive effect of shrub cover and saturation, and a negative effect of canopy cover as the three model variables most strongly related to Dunn’s salamander captures (Table 7). In the single best model for Dunn’s salamanders, an increase of 1% in shrub cover was associated with a 1.3% (95% CI, 0.48–2.12) increase in median number of captures, holding other variables constant. Likewise, an increase in canopy cover of 1% resulted in a 1.2% (95% CI, 0.1–2.34) decrease in median captures, and a change from dry to saturated conditions resulted in a 5.4-fold (95% CI, 3.17–9.24) increase in captures.

Western red-backed salamander

Log-linear models for western red-backed salamander reflected hypotheses that captures would be related to surface moisture, organic substrates, large substrate, down wood, and overstory characteristics (Appendix A, Table A3). Model PV7, including variables for the effect of saturation and large substrate, was selected as the most parsimonious model by QAICc. Akaike model weights suggested that this model was only 1.42 times more likely to be the best fit to the data than its closest competitor. Two other models were within 2 QAICc units of the top-ranked model (Table 6). The null model was ranked 23rd out of 30 models ($\Delta\text{QAICc} = 14.93$, Table A3), implying support for variables from the best models. There was a moderately strong relationship between model predictions and observed values, without outlying residuals. However, the best models had

Table 6. QAICc model selection and ranking results for sets of log-linear regression models (with $\Delta\text{QAICc} \leq 2$) predicting amphibian captures as a function of environmental variables for five species.

Model No.	Model	<i>k</i>	ΔQAICc	<i>w</i>	Dev/df	Estimated slope parameters (95% CI)
Southern torrent salamander						
RV18	GRADE* + HEATNDX + DISTRIDG + SATUR*	5	0	0.844	1.48	$\beta_1 = -7.543$ (–8.607 to –6.502) $\beta_2 = 0.024$ (0.002–0.046)* $\beta_3 = -0.469$ (–0.977 to 0.039) $\beta_4 = -0.094$ (–0.532 to 0.345) $\beta_5 = 3.937$ (3.184–4.69)*
Dunn's salamander						
PD11	SHRUBS* + CCTOT* + SATUR* + LRGSUB	5	0	0.903	1.33	$\beta_1 = -5.375$ (–6.484 to –4.306) $\beta_2 = 0.013$ (0.005–0.021)* $\beta_3 = -0.012$ (–0.024 to –0.001)* $\beta_4 = 1.689$ (1.154–2.224)* $\beta_5 = 0.006$ (–0.004 to 0.016)
Western red-backed salamander						
PV7	SATUR* + LRGSUB*	3	0	0.337	1.63	$\beta_1 = -4.63$ (–4.872 to –4.391) $\beta_2 = -0.892$ (–1.366 to –0.440)* $\beta_3 = 0.013$ (0.006–0.021)*
PV19	GRADE* + AREA* + HEATINDEX + DISTC + LN(DISTRIDG)	6	0.708	0.237	1.62	$\beta_1 = -5.127$ (–5.648 to –4.615) $\beta_2 = 0.036$ (0.017–0.055)* $\beta_3 = -0.307$ (–0.51 to –0.103)* $\beta_4 = 0.127$ (–0.4 to 0.655) $\beta_5 = 0.006$ (–0.009 to 0.021) $\beta_6 = 0.006$ (–0.325 to 0.337)
PV15	LRGSUB* + SATUR* + RDHW + CCTOT	5	1.729	0.142	1.63	$\beta_1 = -5.078$ (–6.081 to –4.132) $\beta_2 = 0.016$ (0.006–0.024)* $\beta_3 = -0.946$ (–1.432 to –0.460)* $\beta_4 = -0.008$ (–0.022 to 0.005) $\beta_5 = 0.006$ (–0.005 to 0.018)
Clouded salamander						
AF16	GEOSRF*	3	0	0.31	1.38	$\beta_1 = -5.33$ (–5.784 to –4.942) $\beta_2 = \text{categorical*}$
AF19	GEOSRF* + SATUR + LN(BA70)* + WOODFREQ + LRGSUB	7	0.840	0.204	1.34	$\beta_1 = -7.004$ (–8.84 to –5.299) $\beta_2 = \text{categorical*}$ $\beta_3 = 0.806$ (–0.119 to 1.731) $\beta_4 = 0.437$ (0.01–0.864)* $\beta_5 = 0.094$ (–0.748 to 0.936) $\beta_6 = -0.006$ (–0.021 to 0.01)
AF17	GEOSRF* + AREA + GRADIENT + HEATINDX	6	1.811	0.125	1.36	$\beta_1 = -4.526$ (–5.39 to –3.684) $\beta_2 = \text{categorical*}$ $\beta_3 = -0.047$ (–0.252 to 0.158) $\beta_4 = -0.024$ (–0.054 to 0.006) $\beta_5 = -0.523$ (–1.191 to 0.144)
Ensatina						
EE4	RDIN* + CCTOT	3	0	0.194	1.21	$\beta_1 = -8.348$ (–10.686 to –6.32) $\beta_2 = 0.019$ (0.006–0.031)* $\beta_3 = 0.025$ (–0.002 to 0.052)

Table 6 (*concluded*).

Model No.	Model	<i>k</i>	ΔQAICc	<i>w</i>	Dev/df	Estimated slope parameters (95% CI)
EE10	RDSHE* + CCTOT + LITTER	4	0.361	0.162	1.2	$\beta_1 = -7.248$ (−9.524 to −5.277) $\beta_2 = 0.019$ (0.007–0.031)* $\beta_3 = 0.019$ (−0.001 to 0.051) $\beta_4 = -0.156$ (−0.587 to 0.274)
EE21	RDIN* + CCTOT* + LITTER + STABLE	5	0.794	0.13	1.19	$\beta_1 = -8.33$ (−10.83 to −6.16) $\beta_2 = 0.015$ (0.002–0.029)* $\beta_3 = 0.026$ (0.001–0.054)* $\beta_4 = -0.368$ (−0.868 to 0.055) $\beta_5 = 0.598$ (−0.388 to 1.696)
EE11	LRGSUB* + RDHW + SATUR	4	0.810	0.129	1.2	$\beta_1 = -4.964$ (−5.34 to −4.617) $\beta_2 = -0.037$ (−0.063 to −0.014)* $\beta_3 = 0.014$ (−0.007 to 0.035) $\beta_4 = -1.184$ (−2.971 to 0.603)
EE7	CCTOT* + LITTER + ORGSUB*	4	1.502	0.092	1.21	$\beta_1 = -8.548$ (−11.068 to −6.335) $\beta_2 = 0.025$ (0.001–0.053)* $\beta_3 = -0.3$ (−0.755 to 0.088) $\beta_4 = 0.023$ (0.007–0.039)*
EE20	CCTOT + ORGSUB + DISTC + GRADE	5	1.969	0.072	1.2	$\beta_1 = -7.69$ (−10.358 to −5.29) $\beta_2 = 0.023$ (−0.001 to 0.051) $\beta_3 = 0.016$ (−0.002 to 0.034) $\beta_4 = -0.009$ (−0.037 to 0.015) $\beta_5 = -0.031$ (−0.064 to 0.001)

Note: Models are ordered by increasing ΔQAICc . *k* represents the number of variables in a model (including intercept); *w* is Akaike model weight. Deviance/degrees of freedom (Dev/df) is provided as a model fit statistic. Asterisks indicate statistically significant environmental parameters. Sample size (*n*) is 126 for southern torrent salamander, Dunn's salamander, and ensatina; 189 for western red-backed and clouded salamander. Environmental parameter are described in Table 2.

moderately high deviance/df, and there was no clearly superior single model or variables. Thus although there was strong support for several individual variables, the models tested may be only moderately useful in describing relationships between western red-backed salamander captures and environmental variables.

Normalized parameter predictor weights supported positive relationships between western red-backed captures and large substrate, basin gradient, and heat load index, and negative relationships with saturation and basin area as the five most important variables in the model set (Table 7). Two of three models with $\Delta\text{QAICc} < 2$ had a negative relationship between captures and saturation, and a positive relationship with large substrates (Table 6). In the highest ranked model (PV7), a change from dry to saturated conditions was associated with a 2.44-fold decrease (95% CI, 1.55–3.92) in median number of captures, holding large substrate constant. For model PV7, an increase of 1% in large substrate cover was associated with a 1.5% (95% CI, 0.6–2.1) increase in median captures, holding saturation constant. For model PV19 (Table A3), an increase in basin gradient of 1° was associated with a 3.67% (95% CI, 1.71–5.65) increase in median captures, holding other variables constant. Similarly, a 1 ha increase in basin area was associated with a 35.9% (95% CI, 10.88–66.55) decrease in median captures.

Clouded salamander

Log-linear models for clouded salamander represented hypotheses that captures were related to geomorphic zone, down wood, large substrate, and overstory characteristics (Appendix A, Table A4). The a priori model set supported three closely competing models ($\Delta\text{QAICc} \leq 2$). The most parsimonious model for clouded salamander captures in zero-order basins was a univariate model with a categorical variable for geomorphic surface (Table 6). This model was less than one QAICc unit from its closest competitor and only 1.52 times more likely to be the best fit to the data in the model set. The null model was ranked 14th out of 31 ($\Delta\text{QAICc} = 7.83$), suggesting that measured variables had relatively weak relationships with clouded salamander captures. A priori models had moderate deviance/df (1.34–1.37), a weak relationship between model predictions and observed values, and lacked a clearly superior a priori model or distinct subset of important variables other than geomorphic surface. This suggests that models of the relationships between clouded salamander captures and measured variables had only moderate utility.

Normalized parameter predictor weights supported changes in geomorphic surface (a categorical variable), a negative relationship with basin area, and a positive relationship with saturation as the most important parameters in the

Table 7. Variable parameter predictor weights from log-linear models for five salamanders.

Environmental variable	Southern torrent salamander	Dunn's salamander	Western red-backed salamander	Clouded salamander	Ensatina
Geomorphic variable					
Geomorphic surface				0.273	
Basin area		0.006	0.131	0.125	
Basin gradient	0.438		0.142	0.094	
Heat load index	0.438		0.131	0.085	
Ridge distance	0.063	0.003	0.072		
Distance from center			0.101		
Fluvial and hillslope variable					
Saturation	0.058	0.101	0.131	0.102	0.056
Deposition		0.002			
Stability				0.088	0.038
Large substrates	0.004	0.097	0.156	0.053	0.162
Litter depth					0.068
Organic substrate					0.055
Overstory variable					
Canopy cover		0.231	0.028		0.093
Large overstory		0.010	0.0291	0.0851	
Relative density within geomorphic surfaces					0.203
Relative density of hardwoods		0.001	0.079		0.162
Relative density of western hemlock					0.101
Down wood volume		0.003		0.024	0.062
Down wood frequency				0.071	
Shrub cover		0.545			

Note: Parameter predictor weights represent the sum of model weights for all models containing the variable, corrected for the total number of models in which the variable appears, normalized to sum to 1.0, as per Stoddard (2001). Only variables from models within the 0.95 confidence set of model weights (Burnham and Anderson 2001) are presented.

model set (Table 7). The three top models ($\Delta\text{QAICc} \leq 2$) all included the geomorphic surface variable (Table 6). For the single best model, a change from valley to headmost area was associated with a 36% (95% CI, 14.8–98.5) increase in median capture rates. Differences in captures between other geomorphic zones were not significant. For model AF19, a twofold change in basal area of trees over 70 cm was associated with a 35.16% (95% CI, 0.67–81.47) increase in median capture rates, holding other variables constant (Table 6).

Ensatina

Models for ensatina reflected hypotheses that captures would be directly or indirectly linked to surface moisture, substrate, down wood, and overstory characteristics (Appendix A, Table A5). Only headmost areas and slopes were modeled, since only five captures occurred in valleys. The a priori model set supported six closely competing models ($\Delta\text{QAICc} \leq 2$). The most parsimonious model for ensatina captures in zero-order basins (EE4) had a model weight of 0.19 and was only 1.2 times more likely to be the best fit to the data than its closest competitor. The null model was ranked 16th out of 29 ($\Delta\text{QAICc} = 9.73$), suggesting that the variables in the best models had moderately strong relationships to ensatina captures. The top a priori models had deviance/df < 1.25; however, relationships between model predictions and observed values were relatively weak, suggesting only moderate model fit.

Normalized parameter predictor weights supported a positive relationship between ensatina captures and relative

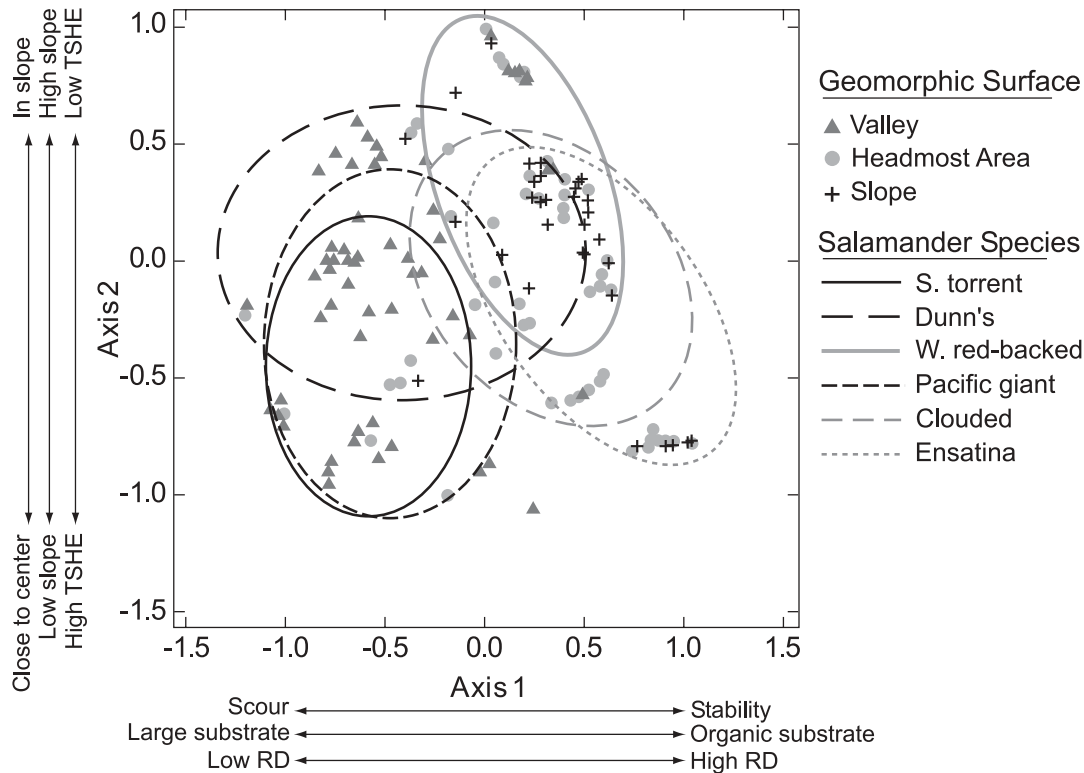
density within geomorphic surfaces, relative density of hardwoods, relative density of hemlock, and canopy cover, and a negative relationship with large substrate as the five most important variables in the model set (Table 7). For the top six models ($\Delta\text{QAICc} \leq 2$), five parameters were statistically significant in at least one model (Table 6). Relative density within geomorphic surfaces occurred in two of the top models, with a transformed coefficient range of 0.002 to 0.031. In the highest ranked model (EE4), a one unit increase in relative density within geomorphic surfaces was associated with a 1.87% increase (95% CI, 0.57–3.18) in median capture rates, holding other variables constant. For model EE10, an increase of one unit in relative density of hemlock was associated with a 1.92% (95% CI, 0.65–3.20) increase in median ensatina captures, holding other factors constant.

Composition of amphibian assemblages

Ordination using NMS reduced data on captures of six amphibian species into a few easily interpretable axes (Fig. 3). A three-dimensional NMS solution had a stress value of 12.7, which is considered “interpretable” under the stringent criteria developed by Clarke (1993). This three-dimensional ordination was rotated to keep its interpretable portion in two dimensions, and to maximize correlations between axis 1 and the stability variable. Ordination distances in this two-dimensional space had a summed correlation with the original six-dimensional space of 0.727.

Ordination of experimental units (geomorphic surfaces) revealed gradients in amphibian composition in zero-order basins (Fig. 3). Experimental units with high captures of

Fig. 3. Ordination of experimental units in amphibian species-space. Experimental units (points) represent the average of amphibian transects for each geomorphic surface in a basin. Geomorphic surface membership is shown, overlain on points. Ellipses are drawn around points with highest densities of respective species. Directional arrows indicate important environmental gradients identified through correlation analysis. For geomorphic surfaces, $n = 176$. TSHE, relative density of western hemlock.



southern torrent, Dunn's, and Pacific giant salamander were tightly coupled in ordination space. Units with mostly clouded salamander and ensatina captures were situated at the opposite end of the dominant gradient (axis 1). Units with high captures of western red-backed salamander were peripheral in ordination space.

Overlay of environmental variable values on the ordination allowed interpretation of axis gradients and illustrated the relationships between species composition and environmental and geomorphic conditions (Fig. 3). Axis 1 score was positively correlated with stability ($r = 0.611$), relative density within geomorphic surfaces ($r = 0.618$), and overstory basal area ($r = 0.47$), and it was negatively correlated with surface moisture ($r = -0.550$), scour ($r = -0.574$), and large substrate cover ($r = -0.477$). Axis 2 score was weakly positively correlated with basin gradient ($r = 0.284$) and distance from center ($r = 0.199$), and it was negatively correlated with relative density of hemlock ($r = -0.212$). These correlations were all significant ($p < 0.001$). Units with high captures of southern torrent, Dunn's, and Pacific giant salamander occurred in areas of the ordination associated with fluvial and (or) hillslope disturbance and surface moisture, usually in valleys and headmost areas. Units with high captures of clouded and ensatina generally had higher stability and dense overstory, mostly in slope and headmost areas. Units with high western red-backed salamander captures occurred in steep areas far from fluvial center, mostly in slope and headmost areas.

Indicator species analysis supported the importance of geomorphic surfaces in structuring amphibian assemblages

in zero-order basins and clarified the hierarchical importance of lateral zones within geomorphic surfaces (Table 8). For the geomorphic surface classification scheme, three species were significant indicators for valleys: Pacific giant (aquatic and terrestrial forms), southern torrent, and Dunn's salamanders. Clouded salamander and ensatina were significant indicators for headmost areas. These species had higher densities in and fidelity to headmost areas than to other geomorphic surfaces, and formed a distinct assemblage associated with this area. Western red-backed salamander was most strongly associated with slopes; however, it had high densities in all three geomorphic surfaces.

Indicator species analysis for the lateral zone classification scheme clarified the hierarchical nesting of lateral differences in amphibian composition within geomorphic surfaces (Table 8). Four species were significant indicators for the 0–2 m lateral zone: Pacific giant (aquatic form), southern torrent, and Dunn's salamanders, and tailed frog. Clouded salamander, ensatina, and western red-backed salamander were not significant indicators for any lateral zone, implying that these species were present across lateral zones in zero-order basins. These results were comparable to contrasts from log-linear models and suggest that these terrestrial-breeding amphibians sort more by geomorphic surface than by proximity to fluvial center.

The geomorphic surface classification had higher summed indicator values than the most similar lateral zone, for each surface and zone compared (Table 8). Multi-response permutation procedure (MRPP) confirmed this result. Amphibian species distributions differed among classes in both classifi-

Table 8. Amphibian assemblages associated with geomorphic surface zones and lateral zones developed using indicator species analysis.

Species	Max. indicator value ^a	<i>p</i> ^b
Geomorphic surfaces		
Valley		
Dunn's salamander	56.7	0.001
Southern torrent salamander	52.7	0.001
Pacific giant salamander (A)	19.4	0.001
Pacific giant salamander (T)	11.3	0.004
Sum of all species ^c	184	
Headmost		
Clouded salamander	29.8	0.002
Ensatina	24.4	0.003
Sum of all species	87	
Slope		
Western red-backed salamander	31.4	0.055
Sum of all species	70	
Lateral zones		
0–2 m		
Southern torrent salamander	57.3	0.001
Dunn's salamander	49.4	0.001
Pacific giant salamander (A)	15.3	0.005
Tailed frog	7.1	0.035
Sum of all species	174	
2–5 m		
Sum of all species	62	
>5 m		
Sum of all species	55	

^aMaximum indicator value is the percentage of perfect indication of a species for the group it was most strongly associated with.

^bThe proportion of shuffled data matrices having maximum indicator values as high as or higher than the original data (Monte Carlo test).

^cSum of indicator values for all species for each class. For geomorphic surfaces, *n* = 176; and for lateral zones, *n* = 166.

cation schemes (*T* values: –20.98 and –27.85, *p* < 0.0001). The geomorphic surface classification scheme had a slightly higher chance-corrected within-group agreement (*A* = 0.153) than the lateral zone scheme (*A* = 0.116). The results of indicator species analysis and MRPP suggest that differences in geomorphic surface may be slightly more important than lateral zone distinctions in structuring amphibian assemblages in zero-order basins.

Discussion

The implementation of buffer protection in western North American riparian areas (Table 1) since the 1950s (Gregory 1997) has modified management in forested landscapes. However, zero-order basins have traditionally been treated as upland forest. If zero-order basins provide unique resources, such as critical habitats for riparian species, management activities in these areas could have adverse effects on biotic resources. Within zero-order basins, our observational study determined the upper limits and spatial patterning of amphibians as well as habitat features associated with their occurrence. These results suggest that amphibians may have unique ties to this portion of the forested landscape. Results from this study may be considered as reference conditions

against which findings from basins with forest management can be weighed. Although the scope of inference for these findings is limited to unmanaged zero-order basins within the study area, our results suggest hypotheses to be tested regarding the role of geomorphic gradients in structuring zero-order basin amphibian assemblages that likely extend from the western portions of northern California to British Columbia. Because models have not been cross validated and because this was an observational study, models should be considered as hypotheses for further testing, not as predictive tools.

Zero-order basins may be important for sensitive amphibians. Although the amphibian species we detected are found throughout the Coast Range of Oregon, four of eight species we observed have a status of concern in all or parts of their ranges in the Pacific Northwest (Table 1). All eight species have been found to have some associations with components of older forest ecosystems, and all but ensatina have been rated to have medium to high viability risk regionally (reviewed in Blaustein et al. 1995).

This study extends the longitudinal range of aquatic and riparian species higher into headwater areas. Zero-order basins were found to support four species traditionally associated with aquatic and riparian habitats: southern torrent, Pacific giant, and Dunn's salamanders, and adult tailed frogs (Nussbaum et al. 1983; Bury et al. 1991; McComb et al. 1993). We observed two amphibian species traditionally associated with upland areas in zero-order basins: clouded salamander and ensatina (Corn and Bury 1991; Welsh and Lind 2002). Information regarding clouded salamander is of particular interest because the habitat relationships of this species are poorly understood. Western red-backed salamander has been found in both upland (McComb et al. 1993) and riparian (Vesely 1997) areas. In our study of zero-order basins, western red-backed salamander had the highest densities of any amphibian in headmost and slope geomorphic surfaces (drier portions of zero-order basins) and did not appear to be a riparian obligate. Pond breeding amphibians such as red-legged frog (*Rana aurora* Baird and Girard), rough skinned newt (*Taricha granulosa* (Skilton)), and (except for one capture) northwestern salamander were not observed in the zero-order basins we studied, although they were observed in the surrounding landscape.

Amphibian detection frequencies in this study suggest that zero-order basins may represent important habitat for semi-aquatic and riparian amphibians, but less important habitats for aquatic and upland species. Estimated densities for southern torrent, Dunn's, western red-backed, clouded, and ensatina salamanders (Table 3) in zero-order basins were higher than captures reported by Vesely (1997) for unmanaged riparian buffers in perennial reaches in the Oregon Coast Range. In contrast, densities of upland amphibians in zero-order basins, particularly western red-backed salamanders, were lower than densities reported by others (Corn and Bury 1991; Davis 1996). Densities for aquatic species (Pacific giant salamander and tailed frog) in zero-order basins were also lower than those suggested for downstream habitats in the Pacific Northwest (Bury et al. 1991). However, caution should be exercised in comparing density results among studies, because of differences in effort, methodology, and sampling design. In our study, capture rates, the response

in most analyses, reflected surface abundance, detectability, and search effort. These components cannot be separated. Thus, our results may overemphasize response of easily captured species and undercount difficult to capture species.

Spatial patterning of amphibians in zero-order basins

The densities of riparian- and upland-associated amphibian species in zero-order basins followed spatial gradients consistent with species natural history and with the restricted nature of microhabitats in these basins. Species with life-history ties to fluvial conditions (Pacific giant, southern torrent, and Dunn's salamanders) occurred farther from ridges (i.e., downstream) than other amphibians. Amphibians requiring perennial flow were restricted to the extreme lower ends of zero-order basins, while southern torrent salamanders occurred in seep habitat above the initiation of fluvial scour and deposition. Pacific giant, southern torrent, and Dunn's salamanders occurred significantly closer to the center of basins than western red-backed and clouded salamanders and ensatinas. Southern torrent salamander, an aquatic species associated with oxygenated flowing systems (Welsh and Lind 1996), was strongly associated with the 0–2 m lateral zone. Dunn's salamander occurred almost exclusively in valleys but had little difference in captures within the first 5 m from basin center, consistent with current understanding regarding its splash-zone life history. Both clouded and western red-backed salamanders had their highest densities in areas 2–5 m from basin center, but indicator species analysis found no significant indicator species for the 2–5 m or >5 m zones. These results suggest that the highest amphibian diversity in zero-order basins occurs in areas close to the fluvial center, at least during the time period in which we surveyed. Areas >5 m from basin centers supported amphibian faunas similar to those in surrounding upland areas. These results are comparable to preliminary findings of Olson et al. (2000), who found strong reductions in relative humidity and changes in other environmental variables outside of a zone 15 m from center in headwater stream inner gorges. These cool, moist zones appear to be amphibian diversity hotspots.

Geomorphic surfaces integrate longitudinal (valley vs. headmost areas) and lateral (valley and headmost areas vs. slopes) differences in amphibian composition. Log-linear regression models showed that southern torrent and Dunn's salamander were much more common in valley floors, less so in headmost areas, and functionally absent from slopes. Indicator species analysis supported riparian species (southern torrent, Dunn's, Pacific giant) as strong indicators for valley geomorphic surfaces, particularly in the 0–2 m lateral zone. Western red-backed salamander was a marginally significant indicator species for slope areas, but there were negligible differences in western red-backed salamander captures among the three geomorphic surfaces. No other species were uniquely associated with slope surfaces.

Indicator species analysis supported clouded and ensatina salamanders as strong indicators for headmost areas. Both clouded salamander and ensatina achieved their highest densities in headmost areas. Headmost areas had the highest amphibian richness and higher densities of riparian species than slope areas. Amphibian diversity in headmost geomorphic surfaces was lower than that in valley surfaces, and

not significantly higher than that in slope areas. These results suggest that headmost areas, drainage areas above scour and deposition, support a marginally distinct, patchily distributed (Gregory et al. 1991) amphibian assemblage, comparable in richness to higher-order riparian systems downstream, inclusive of both riparian and upland species.

Amphibian associations with habitat variables in zero-order basins

Several species–habitat models supported relationships between amphibian taxa and abiotic conditions, while others indicated the importance of late-successional forest characteristics, such as large trees. Southern torrent salamanders were strongly associated with saturation and basin gradient, and weakly positively associated with distance from ridge and large substrate. Welsh and Lind (1996) suggested that at a microhabitat scale, southern torrent salamanders are associated with seep habitats and a mix of coarse substrates. Such conditions occur both above and below the initiation of fluvial scour and deposition in zero-order basins.

Captures of Dunn's salamander were positively associated with saturation, shrub cover, and large substrates, and negatively associated with overstory cover. Vesely (1997) also found positive associations between shrub cover and Dunn's salamander densities, and both Lee (1997) and Vesely (1997) found negative correlations between Dunn's salamander density and coniferous overstory cover in headwater streams. In forested zero-order basins, higher cover of shrubs and low canopy cover may be associated with scarps and recent slumps. These open areas are often associated with fluvial disturbance and moist talus (Naiman et al. 2000).

Clouded salamanders were positively associated with changes from valley to headmost surfaces. Others have found positive association between clouded salamander and talus (Corn and Bury 1991) and down wood (Corn and Bury 1991; Butts and McComb 2000). Although there was not a strong relationship between the volume or frequency of down wood and clouded salamander captures in our study, 108 of 129 captures of clouded salamander were made in, on, or under down wood. Levels of down wood in the unmanaged zero-order basins we investigated were relatively high compared with the range investigated by Butts and McComb (2000); thus, amounts of down wood may not have limited clouded salamander densities in any of the sites studied.

Captures of ensatina were positively associated with organic substrates, overstory density (particularly western hemlock), and distance from fluvial center. These findings are comparable to other studies that showed ensatina was associated with fine woody debris (Nussbaum et al. 1983; Vesely 1997), tree density (Welsh and Lind 2002; Vesely 1997), and upland conditions (Corn and Bury 1989; McComb et al. 1993). The presence of an upland associated species like ensatina in zero-order basins, including moderate densities in areas <5 m from fluvial center, reinforces the intermediate position of zero-order basins between riparian and upland systems.

The relationships we found between individual amphibian species and environmental variables in zero-order basins were consistent with amphibian studies conducted in other geomorphic contexts. However, in zero-order basins, fluvial

and upslope habitat elements were more spatially compressed, closely juxtaposed, and patchy (Gregory et al. 1991; Pabst and Spies 1998), at both small and intermediate scales. This appeared to lead to closely juxtaposed and less distinct amphibian assemblages. The effects of this juxtaposition are clear in ordination results, with the overlap in species composition in slope and headmost area units, and in the indistinct lateral assemblages produced using indicator species analysis.

Conclusions

The role of headwater drainages, including zero-order basins, in forest ecosystems is under investigation in western North America. These areas are important in the transport of inorganic substrate and large wood down gradient to higher-order systems, principally through debris flows (Benda 1990; May and Greswell 2003). Headwater systems influence downstream water quality (Beschta et al. 1987; Forest Ecosystem Management Team 1993) and support distinct invertebrate (Dietrich 1992) and fish (Hubble 1994) faunas. Preliminary studies have shown distinct amphibian faunas in managed headwater Oregon Coast Range streams (Olson et al. 2000; Stoddard 2001) and intermittent Oregon Cascade Ranges streams (Lee 1997). This study is the first to document the composition and habitat associations of amphibian assemblages in unmanaged zero-order basins.

In considering the results of log-linear regression models and indicator species analysis, unmanaged zero-order basins in the south-central Oregon Coast Range appeared to support three amphibian assemblages: (i) a valley assemblage consisting of seep, splash-zone, and aquatic species (southern torrent, Dunn's, and Pacific giant salamander), associated with fluvially disturbed areas 0–5 m from the basin center; (ii) a headmost assemblage, composed of clouded salamander (especially in areas 2–5 m from center) and ensatina (in drier areas); and (iii) a slope assemblage, consisting of western red-backed salamander in transition slope areas (2–5 m lateral zone) and ensatina in midslope, drier areas (>5 m lateral zone). However, although there were distinct differences in the densities of amphibian species across geomorphic surfaces, each species was observed in each of the surfaces. Western red-backed salamander, for example, was ubiquitous. Also, the distinctness of these assemblages may depend on season. During sustained periods of high relative humidity and moderate temperature, or during potential dispersal seasons of the species' life history, these assemblages may become indistinct. During summer months, amphibian assemblages may become more compressed if species move closer to fluvial centers. Finally, habitat use may vary during the life history of most forest amphibians in the Pacific Northwest, and potential dependencies on portions of the forest landscape for particular life-history functions (e.g., breeding, foraging, dispersal, summer–winter refugia) are unknown.

Although amphibian usage of basin areas above sustained fluvial scour and deposition has been considered (Olson et al. 2000), the upper limits of riparian species in drainage basins have not been well defined. From this study, it appears that at least two fluvially dependent species, southern torrent and Dunn's salamanders, penetrate drainage basins

above the start of scour and deposition and higher into headwater areas than previously known. These species had mean proximity to ridgelines of approximately 170 m and minima of 36 and 46 m from ridgelines (respectively), whereas the distance to start of flow averaged over 180 m in zero-order basins.

Geomorphic surfaces in zero-order basins are unique, shaped by distinct fluvial and hillslope disturbance regimes. These landforms provide a unique patch size and spatial arrangement of habitat features on the forested landscapes of the Pacific Northwest. The spatially compressed, closely juxtaposed, and patchy habitat features associated with geomorphic surfaces in zero-order basins may lead to amphibian assemblages that are less distinct but comparable in richness and abundances to those of larger riparian drainages.

Forest management applications

Buffers have been suggested as techniques to minimize impact to stream-dependent (Kelsey 1995) and terrestrial (Vesely 1997) riparian amphibians. Currently, buffers are not required in zero-order basins. The results of this study show that riparian-associated amphibians (e.g., southern torrent salamander) and sensitive amphibians (e.g., clouded salamander) utilize zero-order basins, and that the densities of these species are related to habitat variables, including both relatively invariant parameters (e.g., basin gradient and aspect) and parameters affected by management such as large substrates and overstory conditions. Management activities that affect substrate and overstory composition in headwater areas have been shown to have negative effects on amphibian densities (Corn and Bury 1989; Kelsey 1995). Considering these findings, where protection of amphibian species in zero-order basins is a priority, we suggest that development of reserved areas within a landscape context might be an effective approach to ensure maintenance of amphibian species in forested landscapes. Cissel et al. (1998, 1999) have developed landscape-level (subdrainage-level) reserve concepts, but without considering zero-order basins as specific design elements.

If zero-order basins were included in subdrainage reserves, both patch reserves (including entire zero-order basins) and linear buffers might be useful in minimizing the effects of management activities on amphibian species. Patch reserves, encompassing entire zero-order basins and having species objectives as a key priority, would minimize impacts from timber harvest and road installation on (i) species associated with headmost areas (clouded salamander); (ii) amphibian species utilizing drier portions of zero-order basins (ensatina); and (iii) species associated with fluvial environments (southern torrent, Dunn's, and Pacific giant salamanders). Patch reserves could also provide connectivity between zero-order basins across ridgelines. Linear buffers established along the longitudinal axes of zero-order basins could provide refugia and aquatic connectivity for amphibian species associated with fluvial environments, and upland species distributed across zero-order basins, but having distinct peaks in density in the lower transition slope (western red-backed and clouded salamanders). The dimensions of reserved areas in zero-order basins could be designed to minimize management effects on fluvial and hillslope distur-

bance regimes and associated microhabitat features such as seeps, talus piles (Welsh and Lind 2002), and down wood aggregations. Consideration of microclimatic gradients associated with zero-order basin geomorphology and edge effects associated with adjacent forest management also may be needed. Zero-order basins are much smaller than the riparian systems downstream, and they occur in steep areas frequently not amenable to forestry; thus, establishment of zero-order basin refugia likely would require a smaller modification of management activities than traditional riparian management.

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Appendix A. Amphibian QAICC model sets

Table A1. A priori models describing southern torrent salamander captures as a function of environmental variables, as well as covariate and null models.

Model rank	Model No.	Ecological model	k^a	QAICc	Δ QAICc	w^b	Cumulative w
1	RV18*	GRADE + HEATNDX + DISTRIDG + SATUR	5	7.264	0.000	0.844	0.844
2	RV1	SATUR	2	12.314	5.050	0.068	0.912
3	RV6	SATUR + LRGSUB	3	14.368	7.104	0.024	0.936
4	RV13	SATUR + LRGSUB + SHRUBS + RDIN	5	14.89	7.626	0.019	0.954
5	RV11	SATUR + LRGSUB + RDHW	4	15.405	8.140	0.014	0.969
6	RV8	SATUR + LRGSUB + LN(BA70)	4	15.983	8.719	0.011	0.980
7	RV14	SATUR + LRGSUB + CCTOT + FERNS + LN(BA70)	6	16.283	9.019	0.009	0.989
8	RV17	SATUR + LRGSUB + DISTRIDG + AREA	5	16.833	9.569	0.007	0.996
9	RV9	SATUR + LRGSUB + LM3HA + LN(BA70)	5	18.126	10.862	0.004	>0.999
10	RV10	MOISTR + LRGSUB + LITTER + RDTSH	5	74.102	66.838	<0.001	
11	RV7	MOISTR + SCOUR + DEPOSIT	4	79.276	72.012		
12	RV15	MOISTR + LRGSUB + DISTRIDG + CCTOT + RDIN	6	82.922	75.658		
13	RV12	MOISTR + LRGSUB + SCOUR + LN(M3HA) + LN(BA70)	6	83.522	76.258		
14	RV19	DISTRIDG + AREA + RDIN	4	107.383	100.119		
15	RV4	LITTER	2	125.486	118.221		
16	RV20	DISTRIDG + SCOUR + DEPTH + LN(BA70) + AREA	6	141.492	134.228		
17	RV5	SCOUR + DEPOSIT	3	151.245	143.981		
18	RVN2	DAY + RH + TEMPF	4	166.418	159.154		
19	RV16	DISTRIDG + GRADE + HEATNDX + DEPTH + AREA	6	166.509	159.245		
20	RVN1	DAY + RH + TEMPF + ELEV + DISTOCN	6	168.057	160.793		
21	RVN6	TEMPF	2	171.164	163.899		
22	RV3	DISTRIDG	2	171.361	164.097		
23	RVN3	DAY	2	172.276	165.012		
24	RV2	LRGSUB	2	176.303	169.039		
25	RVN5	RH	2	177.567	170.303		
26	RV0		1	183.454	176.190		
27	RVN4	AGE	2	183.801	176.537		

Note: The global model was over parameterized and was not used in model ranking. This model included the following variables: LRGSUB, SATUR, BA70, CWD3HA, DEPTH, AREA, GRADE, HEATNDX, RDTSH, DISTRIDG, CCTOT, SHRUBS, FERNS, RDHW, DEPOSIT, DAY, RH, TEMPF, ELEV, DISTOCN, AGE. Model RV0 is the null model and RVN1–RVN5 are the covariate models. Model parameters are described in Table 2. Asterisks indicate models with Δ QAICc ≤ 2 .

^aNumber of parameters, including intercept (not shown).

^bModel weighting.

Table A2. A priori models describing Dunn's salamander captures as a function of environmental variables.

Model rank	Model No.	Ecological model	k^a	QAICc	Δ QAICc	w^b	Cumulative w
1	PD11*	SHRUBS + CCTOT + SATUR + LRGSUB	5	112.43	0.000	0.903	0.903
2	PD8	SATUR + LRGSUB + CCTOT + LN(BA70)	5	118.24	5.806	0.050	0.953
3	PD21	LN(DISTRIDG) + SATUR + LN(BA70) + AREA	5	120.08	7.644	0.020	0.973
4	PD6	SATUR + DEPOSIT	3	121.99	9.555	0.008	0.980
5	PD10	SATUR + LRGSUB + LN(BA70) + LN(M3HA)	5	123.05	10.621	0.004	0.985
6	PD1	SATUR	2	123.44	11.002	0.004	0.988
7	PD13	SATUR + LRGSUB + LN(DISTRIDG) + DEPOSIT + LN(BA70)	6	123.77	11.340	0.003	0.992
8	PD7	SATUR + LRGSUB	3	123.87	11.432	0.003	0.994
9	PD22	SATUR + LRGSUB + LN(DISTRIDG) + CCTOT + RDHW	6	124.39	11.951	0.002	0.997
10	PD9	SATUR + LRGSUB + FERNS + CCTOT + LN(M3HA)	6	124.67	12.234	0.002	0.999
11	PD14	SATUR + LRGSUB + DEPOSIT + RDHW	5	125.73	13.301	0.001	>0.999
12	PD23	SATUR + LRGSUB + LN(DISTRIDG) + DEPOSIT + LN(M3HA) + LN(BA70) + AREA + GRADE	20	132.06	19.623	<0.001	
13	PD5	SCOUR + DEPOSIT	3	135.76	23.329		
14	PD15	LITTER + LN(BA70) + RDTSH	4	139.56	27.131		
15	PD16	DEPOSIT + LN(BA70) + RDIN	4	140.31	27.877		
16	PD12	LRGSUB + DEPOSIT + LITTER + RDIN	5	141.35	28.920		
17	PD4	LITTER	2	147.25	34.819		
18	PD18	LN(DISTRIDG) + SCOUR + GRADE + HEATNDX	5	149.57	37.136		
19	PD20	LN(DISTRIDG) + GRADE + LRGSUB + LN(BA70)	5	162.12	49.691		
20	PD2	LRGSUB	2	166.64	54.205		
21	PD3	LN(DISTRIDG)	2	166.68	54.244		
22	PD17	LN(DISTRIDG) + GRADE + HEATNDX + DEPTH + AREA	6	170.80	58.364		
23	PD19	LN(DISTRIDG) + GRADE + HEATNDX + DEPTH + AREA	6	170.80	58.364		
24	PDN1	DAY + RH + TEMPF + ELEV + DISTOCN	6	171.78	59.346		
25	PD0		1	175.07	62.637		
26	PDN5	TEMPF	2	175.19	62.753		
27	PDN3	DAY	2	175.39	62.954		
28	PDN4	RH	2	175.68	63.248		
29	PDN2	DAY + RH + TEMPF	4	178.15	65.714		

Note: Model PD0 is the null model, models PDN1–PDN5 are the covariate models, and model PD23 is the global model. Model parameters are described in Table 2. Asterisks indicate models with Δ QAICc \leq 2.

^aNumber of parameters, including intercept (not shown).

^bModel weighting.

Table A3. A priori models describing western red-backed salamander captures as a function of environmental variables.

Model rank	Model No.	Ecological model	k^a	QAICc	Δ QAICc	w^b	Cumulative w
1	PV7*	SATUR + LRGSUB	3	202.669	0.000	0.337	0.337
2	PV19*	GRADE + AREA + HEATNDX + DISTC + LN(DISTRIDG)	6	203.377	0.708	0.237	0.574
3	PV15*	LRGSUB + SATUR + RDHW + CCTOT	5	204.398	1.729	0.142	0.716
4	PV18	LRGSUB + DISTC + GRADE + LN(BA70)	5	204.913	2.244	0.110	0.826
5	PV14	SATUR + LRGSUB + LN(M3HA) + LN(RD)	5	205.56	2.892	0.079	0.905
6	PV23	SATUR + LN(DISTRIDG) + DISTC + LRGSUB + CCTOT	6	207.986	5.317	0.024	0.929
7	PV24	SATUR + LRGSUB + LN(DISTRIDG)	20	209.065	6.397	0.014	0.943
8	PV9	MOISTR + ORGSUB + CCTOT + RDTShe	5	209.191	6.523	0.013	0.956
9	PVN3	DAY	2	209.595	6.926	0.011	0.966
10	PV21	GEOMSRF + ORGSUB + CCTOT + LN(BA70)	6	209.922	7.253	0.009	0.975
11	PV16	MOISTR + ORGSUB + CCTOT + LITTER	5	210.276	7.607	0.008	0.983
12	PVN2	DAY + RH + TEMPF	4	211.633	8.964	0.004	0.987
13	PV2	SATUR	2	212.034	9.365	0.003	0.990
14	PV8	ORGSUB + CCTOT + LN(BA70) + LITTER	5	212.749	10.080	0.002	0.992
15	PV3	ORGSUB + LITTER	3	212.781	10.112	0.002	0.994
16	PV11	ORGSUB + SCOUR + CCTOT	4	213.269	10.601	0.002	0.996
17	PV6	ORGSUB + LRD	3	214.161	11.492	0.001	0.997
18	PV1	MOISTR	2	214.416	11.747	0.001	0.998
19	PVN1	DAY + RH + TEMPF + ELEV + DISTOCN	6	215.301	12.632	0.001	0.998
20	PVN5	TEMPF	2	215.448	12.779	0.001	0.999
21	PV10	SATUR + SHRUBS + CCTOT + RD	5	217.225	14.556	<0.001	>0.999
22	PVN4	RH	2	217.262	14.593		
23	PV0		1	217.598	14.929		
24	PV17	GEOMSRF	3	218.449	15.781		
25	PV13	LITTER + LN(BA70)	3	218.514	15.845		
26	PV12	STABLE + LN(BA70)	3	219.085	16.416		
27	PV5	LN(RD) + CCTOT	3	220.131	17.462		
28	PV4	LN(DISTRIDG) + DISTC	3	220.913	18.245		
29	PV22	GEOMSRF + MOISTR + LN(M3HA) + CCTOT	6	221.106	18.437		
30	PV20	LN(DISTRIDG) + SCOUR + DEPOSIT	4	222.911	20.242		

Note: Model PV0 is the null model, models PVN1–PVN5 are the covariate models, and model PV24 is the global model. Model parameters are described in Table 2. Asterisks indicate models with Δ QAICc \leq 2.

^aNumber of parameters, including intercept (not shown).

^bModel weighting.

Table A4. A priori model set describing clouded salamander captures as a function of environmental variables.

Model rank	Model No.	Ecological models	k^a	QAICc	Δ QAICc	w^b	Cumulative w
1	AF16*	GEOSRF	3	208.93	0.000	0.310	0.310
2	AF19*	GEOSRF + SATUR + LN(BA70) + WOODFREQ + LRGSUB	7	209.769	0.840	0.204	0.513
3	AF17*	GEOSRF + AREA + GRADE + HEATNDX	6	210.74	1.811	0.125	0.639
4	AF22	STABLE + LN(BA70)	3	211.312	2.383	0.094	0.733
5	AF23	GEOSRF + GRADE + LN(M3HA) + LN(BA70) + AREA	7	212.181	3.251	0.061	0.794
6	AF4	STABLE	2	213.216	4.286	0.036	0.830
7	AF7	CWDM3HA + LN(BA70)	3	213.351	4.422	0.034	0.864
8	AF10	LRGSUB + LN(M3HA) + LN(BA70) + SNAGSHA	5	213.908	4.978	0.026	0.890
9	AF3	LRGSUB	2	214.199	5.269	0.022	0.912
10	AF8	ORGSUB + LN(M3HA) + LN(BA70) + RDIN	5	215.545	6.616	0.011	0.923
11	AF15	LRGSUB + WOODFREQ + LN(BA70) + FERNS + LITTER	6	216.145	7.215	0.008	0.932
12	AF6	WOODFREQ + LRGSUB	3	216.145	7.215	0.008	0.940
13	AF12	ORGSUB + LN(M3HA) + LN(BA70) + SNAGSHA + LITTER	6	216.385	7.455	0.007	0.948
14	AF0		1	216.761	7.831	0.006	0.954
15	AF14	LN(M3HA) + ORGSUB + LITTER + RDTShe	5	216.882	7.952	0.006	0.960
16	AF18	DISTRIDG + DISTC + GRADE + HEATNDX + AREA	6	216.937	8.007	0.006	0.965
17	AF9	LRGSUB + LN(M3HA) + LITTER	4	217.087	8.158	0.005	0.970
18	AF21	DISTRIDG + DISTC + STABLE + LN(M3HA) + GRADE	6	217.448	8.518	0.004	0.975
19	AF5	CWDM3HA	2	217.746	8.816	0.004	0.979
20	AF2	SATUR	2	217.966	9.036	0.003	0.982
21	AFN4	RH	2	218.051	9.121	0.003	0.985
22	AFN5	TEMPF	2	218.666	9.736	0.002	0.988
23	AF11	LN(M3HA) + LN(BA70) + CCTOT + SHRUBS + FERNS	6	218.694	9.764	0.002	0.990
24	AFN3	DAY	2	218.704	9.774	0.002	0.992
25	AF24	DISTRIDG + DISTC + CCTOT + LRGSUB + LN(M3HA)	6	218.71	9.780	0.002	0.995
26	AF1	WOODFREQ	2	218.802	9.872	0.002	0.997
27	AF13	SATUR + LRGSUB + WOODFREQ + RDHW	5	218.946	10.017	0.002	0.999
28	AFN2	DAY + RH + TEMPF	4	220.559	11.629	0.001	>0.999
29	AFN1	DAY + RH + TEMPF + ELEV + DISTOCN	6	223.717	14.788	<0.001	
30	AF25	GEOSRF + SATUR + LRGSUB + LN(BA70) + CWDM3HA + AREA + DISTOCN + GRADE + HEATNDX + RDTShe + DISTRIDG + CCTOT	23	234.893	25.963		

Note: Model AF0 is the null model, models AFN1–AFN5 are the covariate models, and model AF25 is the global model. Model parameters are described in Table 2. Asterisks indicate models with Δ QAICc ≤ 2 .

^aNumber of parameters, including intercept (not shown).

^bModel weighting.

Table A5. A priori model set describing ensatina captures as a function of environmental variables.

Model rank	Model No.	Ecological model	k^a	QAICc	Δ QAICc	w^b	Cumulative w
1	EE4*	RDIN + CCTOT	3	180.503	0.000	0.194	0.194
2	EE10*	RDTSHE + CCTOT + LITTER	4	180.864	0.361	0.162	0.356
3	EE21*	RDIN + CCTOT + LITTER + STABLE	5	181.297	0.794	0.130	0.486
4	EE11*	LRGSUB + RDHW + SATUR	4	181.312	0.810	0.129	0.616
5	EE7*	CCTOT + LITTER + ORGSUB	4	182.005	1.502	0.092	0.707
6	EE20*	CCTOT + ORGSUB + DISTC + GRADE	5	182.472	1.969	0.072	0.780
7	EE2	ORGSUB	2	183.562	3.059	0.042	0.822
8	EE6	ORGSUB + LITTER	3	183.805	3.303	0.037	0.859
9	EE9	ORGSUB + LITTER + DISTC + CCTOT	5	183.964	3.462	0.034	0.893
10	EE8	ORGSUB + LITTER + CCTOT + LN(M3HA)	5	184.084	3.581	0.032	0.926
11	EE17	DISTC + STABLE + GRADE	4	184.213	3.710	0.030	0.956
12	EE16	DISTC + ORGSUB + LN(M3HA) + CCTOT + GRADE	6	184.66	4.157	0.024	0.980
13	EE3	SATUR	2	187.554	7.051	0.006	0.986
14	EE12	GEOSRF + GRADE + HEATNDX	4	188.263	7.760	0.004	0.990
15	EE18	LITTER + LN(BA70)	3	190.094	9.591	0.002	0.992
16	EE0		1	190.23	9.727	0.002	0.993
17	EE1	LITTER	2	191.049	10.546	0.001	0.994
18	EE22	DISTRIDG + DISTC + CCTOT + LITTER	5	191.072	10.570	0.001	0.995
19	EE15	DISTRIDG + DISTC + GRADE + HEATNDX + AREA	6	191.386	10.883	0.001	0.996
20	EE19	DISTC + DEPTH + AREA + CCTOT	5	191.936	11.433	0.001	0.996
21	EEN5	TEMPF	2	191.952	11.449	0.001	0.997
22	EEN3	DAY	2	191.989	11.486	0.001	0.998
23	EE14	GEOSRF	2	192.064	11.561	0.001	0.998
24	EEN4	RH	2	192.208	11.706	0.001	0.999
25	EE23	ORGSUB + LN(M3HA) + AREA + GRADE	19	193.004	12.501	<0.000	>0.999
26	EE5	DISTRIDG + DISTC	3	193.792	13.289		
27	EEN1	DAY + RH + TEMPF + ELEV + DISTOCN	6	194.126	13.623		
28	EEN2	DAY + RH + TEMPF	4	194.387	13.885		
29	EE13	GEOSRF + DEPTH + HEATNDX + AREA	5	196.788	16.285		

Note: Model EE0 is the null model, models EEN1–EEN5 are the covariate models, and model EE23 is the global model. Model parameters are described in Table 2. Asterisks indicate models with Δ QAICc \leq 2.

^aNumber of parameters, including intercept (not shown).

^bModel weighting.